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Description of the *Antistrophus rufus* (Hymenoptera: Cynipidae) Species Complex, Including Two New Species

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Abstract.—We describe the *Antistrophus rufus* species complex of gall wasps, including a redescription of ***A. rufus* Gillette** and descriptions of two new species: ***A. meganae* Tooker and Hanks** and ***A. jeanae* Tooker and Hanks.** Larvae of the three species develop in stem galls of different, but congeneric asteraceous plant species that are endemic to tallgrass prairies of midwestern North America, *A. rufus* in *Silphium laciniatum* L., *A. meganae* in *S. terebinthinaceum* Jacquin, and *A. jeanae* in *S. perfoliatum* L. Adults of the three species are very similar morphologically, but differ in structure of the antennae, length of ovipositors, depth of galls in plant tissues, and mass of mature larvae. An allozyme study confirmed that wasps from the three plant species are reproductively isolated from one another.

Antistrophus Walsh 1869 (Cynipidae: Aylacini) is a Nearctic genus currently comprising at least eight species, all of which form galls in asteraceous plants (Burks 1979, Nieves-Aldrey 1994). Six species form galls in species of *Silphium* and *Lygodesmia* that are endemic to tallgrass prairies of midwestern North America (Burks 1979, Gleason and Cronquist 1991). Larvae of *Antistrophus rufus* Gillette feed in small, single-chambered, ellipsoid galls (~3 mm in length) in flowering stems of *Silphium* species that do not affect the stem surface and so are not discernible externally (Gillette 1891, Beutenmüller 1910, Tooker et al. 2002, Tooker and Hanks 2004a, b, c).

Antistrophus rufus was originally described from specimens reared from *Silphium laciniatum* L. (Gillette 1891), but the species name also has been applied to specimens from *S. terebinthinaceum* Jacquin, *S. perfoliatum* L., and *S. integrifolium* Michaux (Beutenmüller 1910). In our studies of the ecology of *A. rufus* in prairies of central Illinois, we found evidence of reproductive isolation of populations inhabiting stems of *S. laciniatum* and *S. terebinthinaceum* due to phenological differences between host plants (Tooker et al. 2002). Wasps from the two plant species mate assortatively when brought into contact (unpublished data), and males preferentially respond to plant volatiles associated with their natal host species (Tooker et al. 2002). Allozyme studies confirmed that wasp populations inhabiting *S. laciniatum* and *S. terebinthinaceum* were reproductive isolated from one another, and a Nei's genetic distance of 0.56 further indicated that the populations actually represent different species (Tooker et al. 2002).

In this paper, we extend our studies of *Antistrophus* species by including a third population associated with *Silphium perfoliatum*. Differences in phenology between this population and those inhabiting *S. laciniatum* and *S. terebinthinaceum* (see below), again associated with host plant phenology, suggest limited gene flow. We confirm reproductive isolation of the *S. perfoliatum* population with allozyme studies, and also report that wasps from the three *Silphium* species differ in

the morphology of the antennae and ovipositors, depths of galls in host plants, and mass of mature larvae. On the basis of these genetic, morphological, and ecological differences, we conclude that *Antistrophus rufus* comprises a complex of at least three species, *A. rufus* Gillette in *S. laciniatum*, *A. meganae* Tooker and Hanks n. sp. in *S. terebinthinaceum*, and *A. jeanae* Tooker and Hanks n. sp. in *S. perfoliatum*. We provide here descriptions and morphological diagnoses for each species.

METHODS

To compare the morphology of *Antistrophus* populations, we reared adult gall wasps from *Silphium* stems we collected during the winters of 1998–1999 and 2001–2002 from prairie sites in central Illinois. We collected *S. laciniatum* from Fithian Railroad Prairie (FRP, Vermilion Co., N 40° 06.78, W 87° 54.10) and Buckley Railroad Prairie (BRP, Iroquois Co.; N 40° 34.88, W 88° 02.70), *S. terebinthinaceum* from East St. Joseph Railroad Prairie (ESJRP; N 40° 06.77, W 88° 00.48) and Paxton Railroad Prairie (PRP; Ford Co.; N 40° 26.17, W 88° 06.36), and *S. perfoliatum* from BRP and PRP. We measured dimensions of heads and antennae of females using digital photographs (e.g., Fig. 1) produced with microscopy (scanning electron- and compound microscopes) in conjunction with image analysis software (Image-Pro® Plus Version 4.5, Media Cybernetics, Inc., Silver Spring, MD). We dissected ovipositors from ten female wasps from each plant species and measured with a microscope micrometer the length from the tip to the second valvifer (see Fig. 2).

Terminology relating to morphology and wing venation follows Nieves-Aldrey (1994) and descriptions of sculpturing follow Harris (1979). Post-Ocellar Line (POL) is the distance between inner margins of lateral ocelli; Ocell-Ocular Line (OOL) is the distance from outer edge of a lateral ocellus to inner margin of the compound eye. Head height is measured in frontal view from top of stemmaticum to ventral margin of clypeus. Supraclypeal area is the medial area between clypeus and toruli.

To study how gall dimensions and mass of wasp larvae varied across plant species, we dissected stems of *S. perfoliatum*, collected in early Spring 2002 from BRP where all three *Silphium* species co-occurred. We extracted mature gall wasp larvae and weighed them, and measured the depth from the stem surface of galls with a microscope micrometer (N = 22 galls in twenty stems). Data for wasps in *S. perfoliatum* were compared with published data for wasps in *S. laciniatum* and *S. terebinthinaceum* (Tooker and Hanks 2004c).

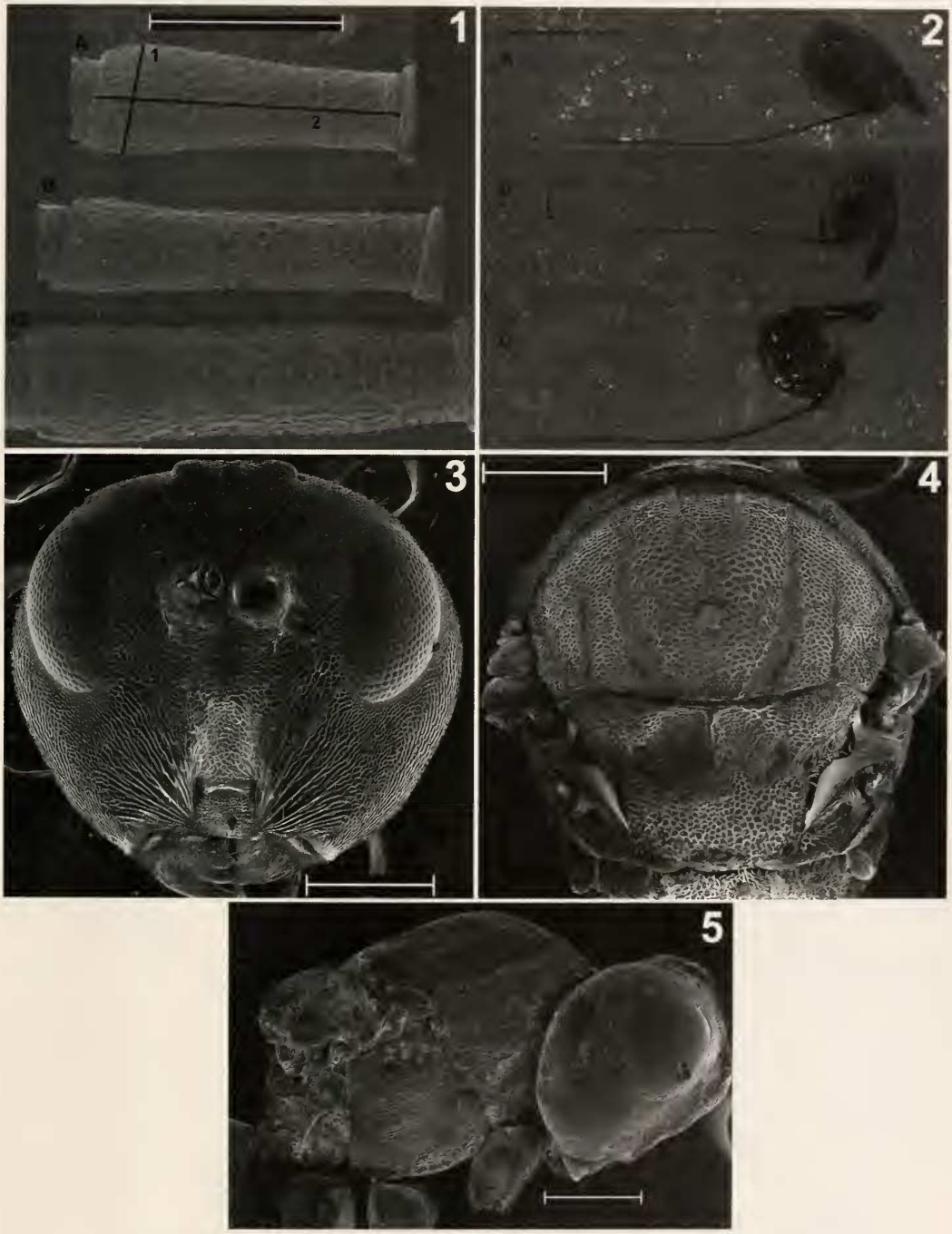
We compared differences between *Antistrophus* populations in means for morphological variables, gall depth, and larval mass with analysis of variance (ANOVA; Wiley 1981). Differences between individual means were tested with the LSD means separation test (Sokal and Rohlf 1995).

For the allozyme analysis, we reared *Antistrophus* adults from stems of *S. perfoliatum* collected at BRP, where all three plant species co-occurred. We conducted cellulose acetate electrophoresis for six loci using methods described by Tooker et al. (2002). We compared allele frequencies for the *S. perfoliatum* population with frequencies for the *S. laciniatum* and *S. terebinthinaceum* populations (from Tooker et al. 2002) using R×C contingency table tests (software ver. 2.1, Bill Engles, University of Wisconsin, Madison).

We present means ± 1 SE throughout.

Antistrophus rufus species complex (Figs. 1–8)

Diagnosis.—Galls developing in cambium and pith of flowering stems of *Silphium laciniatum*, *S. terebinthinaceum*, and *S. perfoliatum*. Second flagellomere longer than first. Notauli evident, but faint ante-



Figs. 1–5. *Antistrophus* species. 1, Second flagellomere of female A) *A. rufus*; B) *A. meganae*; C) *A. jeanae* (scale bar = 100 μm); lines 1 and 2 indicate length and width measurements, respectively. 2, Ovipositors of A) *A. rufus*; B) *A. meganae*; C) *A. jeanae* (scale bar = 1 mm); arrows indicate length measurement. 3, Head of *A. rufus* female (scale bar = 200 μm). 4, Mesonotum and metanotum of *A. rufus* female (scale bar = 200 μm). 5, Head and mesosoma of *A. rufus* male (scale bar = 200 μm).

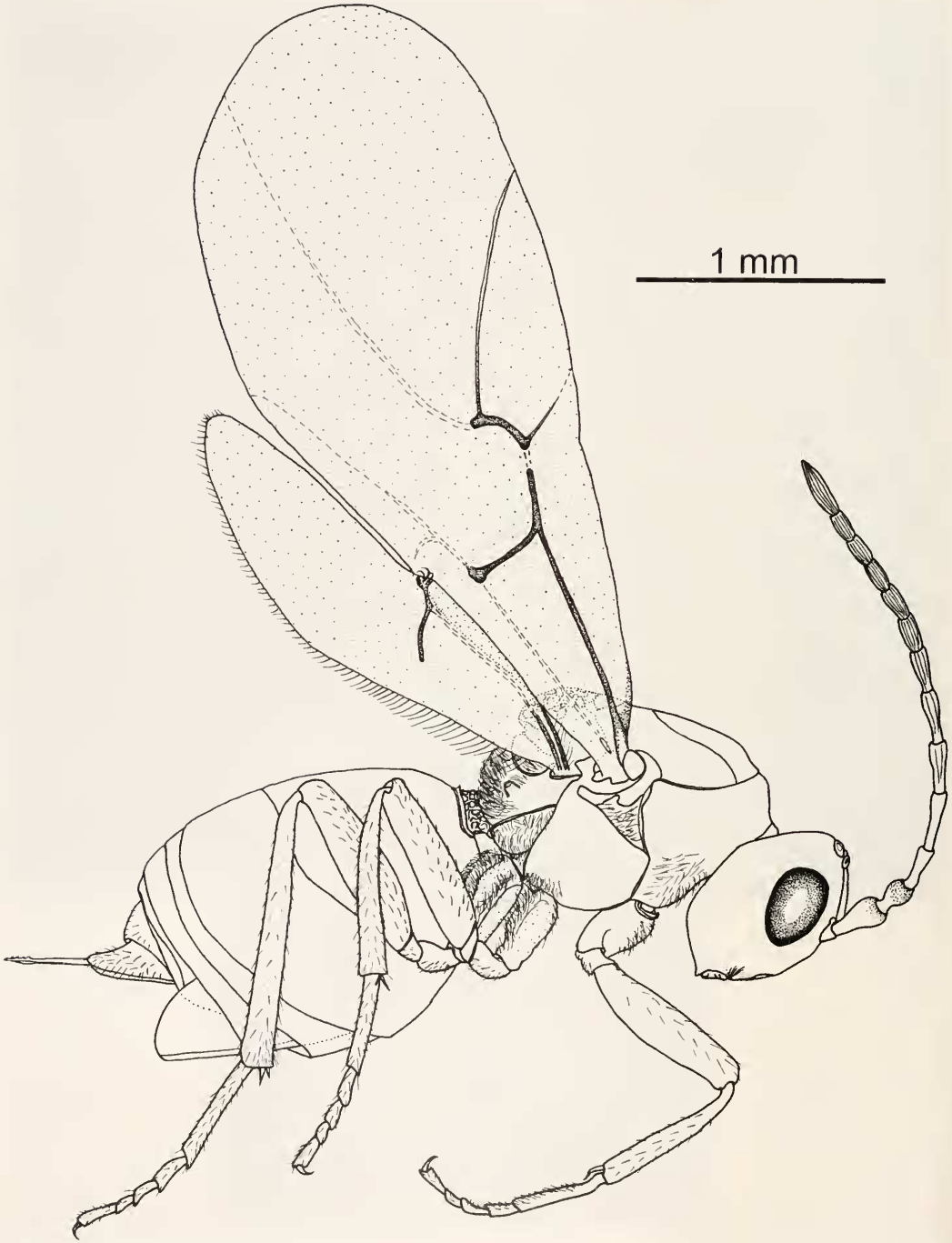


Fig. 6. *Antistrophus rufus* female (scale bar = 1 mm).

riorly. Distinct medial ridge separating scutellar fovae.

Description.—FEMALE. Length 2.6 ± 0.05 mm (Fig. 6). Light brown to amber often with darker (even black) areas in vertex, mesoscutum, and dorsum of metasoma. Antennae and legs same color as body. Head with fine areolate sculpturing and sparsely setose (Fig. 3, 5). Head in dorsal view 1.8× broader than long; in frontal view, 1.4× broader than high; head height 2× compound eye height. POL slightly shorter than OOL and 2× greatest diameter of lateral ocellus. Malar space 0.8× eye height. Face with laterally radiating striae. Supraclypeal area with two pronounced tentorial pits. Antennae 13-segmented and imbricate, distal flagellomere 2× longer then flagellomere 10 (Fig. 7). First flagellomere 0.75× as long as second. Pronotum finely areolate, setose, prominent lateral expansions, and distinct submedial pits (Fig. 4). Mesoscutum finely areolate; anterior fourth of notauli faint, moderately convergent posteriorly. Median mesoscutal impression faint to prominent, but most evident in posterior third. Two faint submedial impressions in anterior fourth and parallel to median mesoscutal impression. Two additional mesoscutal impressions lateral to notali and most evident in posterior third (Fig. 4). Scutellum finely areolate. Scutellar fovae prominent and rounded, separated from each other by distinct medial ridge. Mesopleuron setose and finely areolate (Fig. 5). Propodeum finely areolate and densely setose laterally. Propodeal carinae moderately divergent posteriorly. Metasoma nitid. In lateral view, length of metasoma approximately equal to or slightly shorter than head + mesosoma + propodeum (Fig. 6). Metasomal tergites I and II occupy more than half of abdomen. Hypopygidial spine very short. Ovipositor 2.8 ± 0.08 mm long. Wings hyaline with pale brown venation: R1 and Rs of forewing not extending to wing margin, radial cell open, Rs curved slightly anteriorly (Fig. 6). MALE. Differs from female in shape and size of metasoma (Fig. 8). Antennae longer, with 14 antennomeres (Fig. 7).

GALL. Small (~3 mm in length), ellipsoid, and monothalamous, hidden in cambium and pith of flowering stems of *Silphium*, not evident in external view.

Material examined.—We examined the holotype in the Insect Collection of the Illinois Natural History Survey, Champaign, IL (INHS), which was reared from *S. laciniatum*, as well as 10 females and 5 males that we reared from stems of each of three *Silphium* species (*S. laciniatum*, *S. terebinthinaceum*, and *S. perfoliatum*) collected from prairies in central Illinois (see above). Depositories for specimens are INHS and the National Museum of Natural History, Smithsonian Institution, Washington, DC (NMNH).

Comments.—Previous work revealed that no alleles were shared between gall wasps reared from *S. laciniatum* and *S. terebinthinaceum* (Table 1, Tooker et al. 2002). New data (Table 1) show that gall wasps reared from *S. perfoliatum* had alleles at all six loci that were not represented in wasps from either *S. laciniatum* or *S. terebinthinaceum*, and in fact, 48 and 71% of alleles at loci *MDH* and *ME*, respectively, were unique to *S. perfoliatum* wasps. Moreover, locus *IDH* was fixed for unique alleles in all three wasp populations (Table 1). R-C contingency tables tests for each locus were highly significant ($P < 0.001$), suggesting a lack of gene flow between populations of gall wasps inhabiting different *Silphium* species. These data strongly support the morphological evidence that these populations represent different species.

Antistrophus rufus Gillette
(Figs. 1–8)

Antistrophus rufus Gillette 1891: 195.

Diagnosis.—Distinguished from other species in complex by the following characters: 1) Larvae developing in galls in

Table 1. Allelic frequencies of *A. rufus* species complex reared from stems of *Silphium laciniatum* ("*S. lac.*") and *S. terebinthinaceum* ("*S. ter.*") and *Silphium perfoliatum* ("*S. per.*") from three prairies in central Illinois. Sample sizes are in parentheses. The most anodal band was assigned "A" with electrophoretic mobilities of other bands relative to this band on starch and cellulose acetate gels. Populations are named after their prairies (see Materials and Methods). Data from gall wasp populations in *S. laciniatum* and *S. terebinthinaceum* are from Tooker et al. (2002).

Locus/ mobility	LCP		MP		BRP		
	S. lac. (30)	*S. ter.* (30)	*S. lac.* (10)	*S. ter.* (10)	*S. lac.* (15)	*S. ter.* (15)	*S. per.* (30)
GPI							
A	0.000	0.000	0.000	0.000	0.000	0.000	0.033
B	1.000	0.000	1.000	0.000	1.000	0.000	0.633
C	0.000	1.000	0.000	1.000	0.000	1.000	0.333
PGM							
A	0.000	0.000	0.000	0.000	0.000	0.000	0.058
B	0.000	0.483	0.000	0.550	0.000	0.679	0.250
C	1.000	0.000	1.000	0.000	1.000	0.000	0.462
D	0.000	0.517	0.000	0.450	0.000	0.321	0.231
G3PDH							
A	1.000	0.000	1.000	0.000	1.000	0.000	0.150
B	0.000	1.000	0.000	1.000	0.000	1.000	0.750
C	0.000	0.000	0.000	0.000	0.000	0.000	0.100
MDH							
A	1.000	0.000	1.000	0.000	1.000	0.000	0.069
B	0.000	0.000	0.000	0.000	0.000	0.000	0.034
C	0.000	1.000	0.000	1.000	0.000	1.000	0.448
D	0.000	0.000	0.000	0.000	0.000	0.000	0.448
ME							
A	0.000	0.000	0.000	0.000	0.000	0.000	0.333
B	0.000	0.000	0.000	0.000	0.000	0.000	0.300
C	1.000	0.000	1.000	0.000	1.000	0.000	0.200
D	0.000	0.000	0.000	0.000	0.000	0.000	0.083
E	0.000	1.000	0.000	1.000	0.000	1.000	0.083
IDH							
A	1.000	0.000	1.000	0.000	1.000	0.000	0.000
B	0.000	1.000	0.000	1.000	0.000	1.000	0.000
C	0.000	0.000	0.000	0.000	0.000	0.000	1.000

cambium and pith of flowering stems of *S. laciniatum*, 2) ratio of width/length of first flagellomere intermediate to others in species complex and ratio of width/length of second flagellomere greater than other species in complex (Table 2, Fig. 1), 3) ovipositor longest in complex (Table 3, Fig. 2), 4) size of mature larvae larger than others in species complex (Table 3).

Redescription.—FEMALE. Same as species complex, but ratio of width/length of first flagellomere significantly different and intermediate to that of *A. meganae* and *A. jeanae* (Table 2). Ratio of width/length of second flagellomere significantly larger than both *A. meganae* and *A. jeanae* (Table 2, Fig. 1). Ovipositor significantly longer than in other species in complex (Table 3, Fig. 2). GALL: Depth of galls in stems significantly greater than in other species (Table 3). LARVAE: Mass of mature, overwintering larva significantly greater than in other species (Table 3).

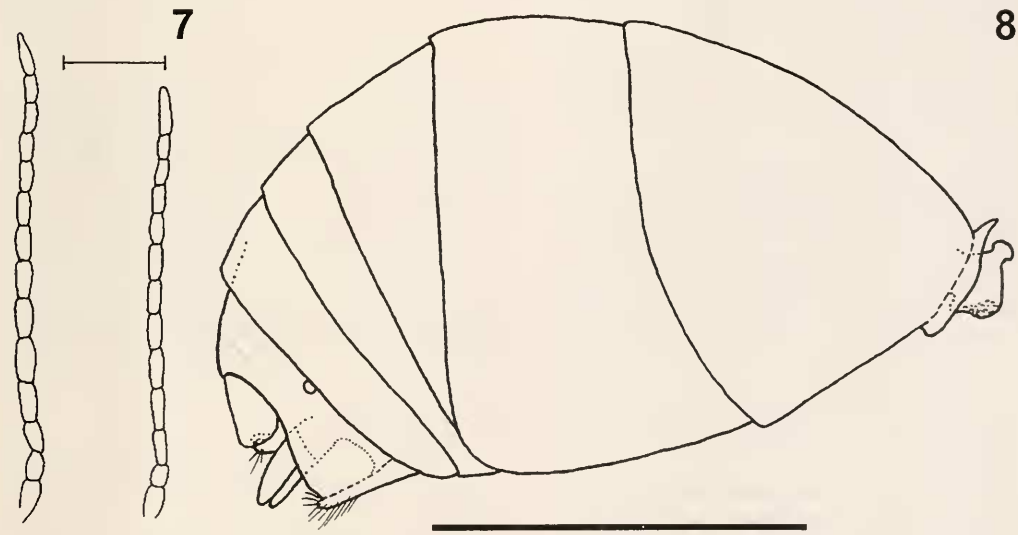
Types.—Holotype at INHS, reared from *S. laciniatum* in Illinois (Gillette 1891). We deposited an additional 10 females and

Table 2. Comparison of width, length, and width/length ratio of first and second flagellomeres (Fig. 1) for three members of the *A. rufus* species complex and ANOVA results. We measured flagellomeres of 20 female wasps reared from each of the three plant species, averaging the values from each antennae to generate mean measurements for each individual. Values within column with different letters are significantly different (LSD $P < 0.05$). Significant P values for ANOVA indicated by "*" ($P < 0.05$), "***" ($P < 0.0001$).

Species	First flagellomere			Second flagellomere		
	Width (mm)	Length (mm)	Width/Length	Width (mm)	Length (mm)	Width/Length
A. rufus	0.08 ± 0.002 b	0.20 ± 0.008 a	0.41 ± 0.011 b	0.09 ± 0.003 a	0.24 ± 0.008 b	0.36 ± 0.006 a
A. meganae	0.08 ± 0.003 b	0.22 ± 0.010 a	0.38 ± 0.001 c	0.08 ± 0.003 a	0.31 ± 0.014 a	0.27 ± 0.005 c
A. jeanue	0.09 ± 0.004 a	0.22 ± 0.007 a	0.43 ± 0.021 a	0.09 ± 0.004 a	0.32 ± 0.011 a	0.29 ± 0.005 b
	$F_{2, 59} = 3.86$*	$F_{2, 59} = 1.42$	$F_{2, 59} = 14.4$***	$F_{2, 59} = 2.06$	$F_{2, 59} = 13.8$***	$F_{2, 59} = 77.7$***

five males at INHS that we reared in Spring 2002 from stems of *S. laciniatum* from FRP (five females and three males) and BRP (five females and two males) in INHS; We also deposited three females and one male from FRP and two females and one male from BRP in NMNH.

Biology.—Larvae develop within galls in flowering stems of *S. laciniatum* (for biology, see Tooker et al. 2002, Tooker and Hanks 2004a). They overwinter in dead stems, pupate in the early spring, and adults emerge in late May through late June. Although adults of both sexes have fully developed and functional wings, they do not fly readily but rather walk, occasionally taking hopping flights to nearby plants. Males emerge before females and search for mates on dead stems of the previous season, guarding areas of stem where females eventually emerge, and driving off competitors by charging or butting with the head. Females mate immediately upon emerging and then move to nearby developing stems of *S. laciniatum* where they oviposit in axils. As many as 20 females oviposit in a stem at the same time and require less than one minute to insert an egg. Egg load upon emergence averages ~165 eggs per female. Densities of galls commonly reach hundreds per stem. Parasitic wasps are



Figs. 7–8. *Antistrophus* species. 7, Antennae of adult A) male and B) female *A. rufus* (scale bar = 500 μm). 8, Metasoma of adult male *A. rufus* (scale bar = 500 μm).

the most significant source of mortality for *A. rufus* larvae with rates of parasitism often exceeding 90% (Tooker and Hanks 2004a). Species of parasitoids reared from *A. rufus* galls include eurytomids (*Eurytoma lutea* Bugbee and an unidentified *Eurytoma* species), an ormyrid (*Ormyrus labotus* Walker), eupelmids (*Eupelmus vesicularis* [Retzius] and two unidentified *Brasema* species), and a pteromalid (unidentified *Homoporus* species; Tooker and Hanks 2004a). Populations of gall wasps are decimated when prairies are burned, but quickly recolonize (Tooker and Hanks 2004b).

Antistrophus meganae Tooker and Hanks, new species
(Figs. 1B, 2B)

Diagnosis.—Larvae developing in galls in cambium and pith of flowering stems of *S. terebinthinaceum*. See description for further details.

Description.—FEMALE. Generally same as others in species complex, but width/length ratio of first and second flagellomeres significantly smaller than in both *A. rufus* and *A. jeanae* (Table 2, Fig. 1B). Ovipositor significantly shorter than in *A. rufus* (Table 3, Fig. 2B). GALL: Significantly closer to the stem surface than other species in complex (Table 3). LARVAE: Mass of mature, overwintering larvae intermediate to that of *A. rufus* and *A. jeanae* (Table 3).

Types.—Holotype reared in June 2002 from stems of *S. terebinthinaceum* collected at ESJRP and deposited in INHS. We deposited nine female and five male paratypes reared from stems of *S. terebinthinaceum* collected in Spring 1999 from PRP (four females, three males) and Spring 2002 from ESJRP (five females and two males) in INHS. We deposited five female paratypes (three from ESJRP, two from PRP) and three male paratypes (two from ESJRP and one from PRP) in NMNH.

Etymology.—Named in honor of Megan Weaver Tooker, spouse of the first author.

Biology.—Similar to *A. rufus*, but larvae develop within galls in flowering stems of *S. terebinthinaceum*. Adults begin emerging from stems in mid-June and continue to emerge for approximately 20 days (Tooker and Hanks 2003a). Females oviposit in stem internodes of *S. terebinthinaceum* after bolting. Similar to *A. rufus*, *A. meganae* larvae can suffer high parasitism rates and the same guild of parasitoids appears to attack both species (Tooker and Hanks 2004a).

Antistrophus jeanae Tooker and Hanks, new species
(Figs. 1C, 2C)

Diagnosis.—Larvae developing in galls in cambium and pith of flowering stems of *S. perfoliatum*. See description for further details.

Description.—FEMALE. Generally same as others in species complex, but width/length ratio of first flagellomere significantly larger, and that of second flagellomere intermediate to other species in complex (Table 2, Fig. 1C). Ovipositor significantly shorter than that of *A. rufus* (Table 3, Fig. 2C). GALL: Intermediate in depth to other species in the complex (Table 3). LARVAE: Mass of mature, overwintering larva significantly lower than in *A. rufus* and *A. jeanae* (Table 3).

Types.—Holotype reared in May 2002 from stems of *S. perfoliatum* collected at BRP and deposited with INHS. We deposited nine female and five male paratypes reared from stems of *S. perfoliatum* collected in Spring 1999 from PRP (four females, three males) and Spring 2002 from BRP (five females, two males) in INHS. We deposited five female paratypes (three from PRP and two from BRP) and three male paratypes (two from PRP and one from BRP) in NMNH.

Etymology.—Named in honor of Jean Michelle Hanks, spouse of third author LMH.

Biology.—Similar to *A. rufus*, but larvae develop within flowering stems of *S. per-*

Table 3. Comparison of ovipositor length, gall depth, and mass of larvae for the *A. rufus* species complex, and ANOVA results. Values within column with different letters are significantly different (LSD $P < 0.05$). Significant P values for ANOVA indicated by "*" ($P < 0.01$), "**" ($P < 0.001$), "***" ($P < 0.0001$).

Species	Ovipositor length (mm)	Gall depth (mm)	Larval mass (mg)
A. rufus	3.19 ± 0.07 a	2.20 ± 0.06 a	2.29 ± 0.13 a
A. meganae	2.54 ± 0.15 b	1.05 ± 0.03 c	1.66 ± 0.09 b
A. jeanae	2.68 ± 0.09 b	1.76 ± 0.10 b	0.88 ± 0.16 c
	$F_{2, 29} = 9.44$*	$F_{2, 24} = 57.9$***	$F_{2, 24} = 6.77$**

foliatum. Adults emerge from stems for a period of about 20 days beginning in mid-May and females oviposit in stem internodes after bolting. Similar to other species in the complex, parasitoids can inflict high levels of mortality on *A. jeanae* larvae.

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